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SEX RATIO OF ODONATA AT EMERGENCE

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Abstract

Final-instar exuviae left at the emergence site by Odonata can provide information of high quality for measuring sex ratio, especially of Anisoptera. Criteria are listed according to which counts of such exuviae are acceptable for this purpose. Records of sex ratio of Odonata, published and unpublished, are critically reviewed, and 194 that meet the listed criteria are presented and analysed. Variability of sex ratio differs widely among taxa but is less in large (N >299) than in small (N = 100-199) collections. Large collections indicate that the proportion of males is greater in Zygoptera than in Anisoptera (respectively 65 and 21% of records featuring >50% males). Because the sex-determination mechanism in Odonata predicts a sex ratio of unity in the zygote, variability and imbalance of sex ratio detected at emergence can plausibly be attributed to differential mortality of eggs and/or larvae and therefore, probably, to differential predation on larvae. The effect, if any, of sex ratio at emergence on reproductive potential of the adult population is unlikely to be significant, except perhaps when, rarely, the number of females is unusually low, thus reducing the size of the next generation.

Introduction

The sex ratio of Odonata has attracted attention from several authors since Tümpel (1899) and Tillyard (1905, 1917). Most observations reviewed by Corbet (1962) and Lawton (1972) have been broadly consistent with Tillyard's tentative conclusion (1917: p. 326) that the number of males and females is approximately equal and that females are slightly in excess.

Because the behaviour of adult males and females differs greatly, it can be nearly impossible to obtain precise measures of sex ratio during the adult stage. Indeed the only time in the life history when sex ratio can be measured without being subject to bias of unknown extent is emergence, when every individual leaves a cast skin on a support close to the water's edge. It is worth emphasising that, by virtue of their size and often high population density in small bodies of water, Odonata offer uniquely favourable opportunities for measuring sex ratio at emergence:

- the emergence period of many species, especially in temperate latitudes, is

relatively brief (a few weeks);
- cast skins (exuviae) normally remain on emergence supports for several days and, especially in Anisoptera, are conspicuous and readily identifiable to species;
- exuviae, if intact, can be sexed unequivocally;
- numbers emerging during one emergence period from a small or medium-sized water body are often manageable for a person making daily collections of exuviae; and
- in many water bodies all emergence supports are, or can be rendered, acces-sible, so that counts can be made virtually exhaustive.

Thus it is often possible to measure sex ratio precisely in the whole population of one species emerging from one habitat. So, if due allowance is made for sources of potential bias, collections of exuviae can provide sex-ratio data of unrivalled quality.

Since the reviews cited above, many accounts of sex ratio at emergence have been published, and we now see merit in critically appraising the data available. Accordingly, our aims in this paper are:
-to present and review records available to date;
-to identify sources of possible bias in field-derived data and to recommend minimum acceptable criteria for ensuring that such data are accurate and comparable;
-to suggest ways of analysing and presenting data;
-to record the range and variability of sex ratio measurements in different taxa; and
-to draw tentative inferences regarding the causes of sex ratio imbalance.

Methods

In this review we include only data that, as far as we have been able to ascertain, satisfy criteria designed to avoid or minimise bias and which accordingly can constitute useful guidelines for field workers. Inspection of published records convinces us that it is necessary to specify all of these criteria. The criteria, which extend and supersede those listed by Corbet (1962: p. 117), follow, accompanied by explanatory notes in square brackets.

Criteria for measuring sex ratio of a given species at emergence by collecting exuviae

1. Species **identification** is secure, and only one species is included.
2. Counts include **only exuviae** and not teneral adults.
3. Collections are all from the **same emergence period** (within one season). [Where information exists, allowance is made for possible heterogeneity due to the existence within the emergence period of time-segregated moieties derived from cohorts with different voltinism, e.g. the second peak of emergence of *Anax imperator* which, when it contains an excess of females, reduces the sex ratio of the annual emerging population (Corbet, 1962:p.117). It will not always be possible to allow for this variable, partly because voltinism within an emergence period is not necessarily uniform, and partly because, even if heterogeneity within an emergence period is confirmed, as in *A. imperator*,

the two moieties probably show temporal overlap.]
4. Collections are all from the **same body of water**.
5. Collections are made in a **standardised way**. [The same effort is devoted on each occasion, preferably to the whole water body, resulting in exhaustive collections, or to a constant part of the water body, resulting in standardised samples.]
6. Only exuviae that can be **sexed** are included in totals. [If possible, the number of exuviae that cannot be sexed is recorded. It is confirmed that such exuviae are not localised in time or place in a way that might distort the record of overall sex ratio.]
7. Collections are made **regularly and frequently** and at about the **same time each day**. [Collections are made preferably daily and no less often than weekly. Weather (e.g. strong or gusty wind or heavy rain) likely to dislodge exuviae is noted in case it jeopardises reliability or continuity of the record.]
8. Collections include the **whole emergence period** in any year. [Collections begin a few days before, and cease a few days after, the emergence period. For bi- or trivoltine species each emergence period is treated separately. Non-seasonal species that lack a restricted emergence period are not eligible for analysis.]
9. The **size of the collection** used to compute the sex ratio exceeds 99 and preferably exceeds 299.
10. Collecting **procedure is described** in the report.
11. The **whereabouts** of the collected material is stated.

We have satisfied ourselves, either from scrutiny of the published account or from correspondence with the author, that each record included in Tables 1-3 meets the criteria listed above closely enough to provide data that are comparable *inter se*. When scrutinising records we were obliged to omit records, in whole or in part, from 28 sources because they failed to meet the criteria in one or more respects.

Table 1. Sex ratios based on totals between 100 and 199. The collecting locality (coll. loc.) is specified if the same author collected the same species in more than one locality in one year.

99<N<200

Taxa	[1] Coll. season	[1] Coll. loc.	% males	N	Chi-squared test, P<	Reference
Anisoptera						
Aeshnidae						
Aeshna cyanea (Müller)	1982		49.4	170		Beutler (1986)
Aeshna cyanea	1984	A	51.5	196		Beutler (1986)
Aeshna cyanea	1988		59.5	182	0.05	H. von Hagen (pers. comm.)
Aeshna grandis (Linnaeus)	1983		38.7	119	0.05	Thompson (1987)
Aeshna juncea (Linnaeus)	1960		48.0	100		Kurata (1966)
Aeshna juncea	1964		49.2	118		Kurata (1966)
Aeshna juncea	1994		42.2	116		W. Clausen (pers. comm.)
Aeshna mixta Latreille	1990		42.3	111		Jahn (1991)
Aeshna subarctica elisabethae Djakonov	1986		51.3	158		W. Clausen (pers. comm.)
Aeshna subarctica elisabethae	1991		44.5	128		W. Clausen (pers. comm.)
Anaciaeschna isosceles (Müller)	1982		49.0	102		Beutler (1986)

Anaciaeschna isosceles	1983		49.0	102		Beutler (1986)
Anax imperator Leach	1983	B	35.1	171	0.001	Beutler (1985, 1986)
Anax imperator	1984	B	50.0	180		Beutler (1985, 1986)
Anax junius (Drury)	1965(S)		48.2	164		Trottier (1966)
Anax junius	1968(S)		48.4	146		Trottier (1971)
Corduliidae						
Cordulia aenea (Linnaeus)	1984		43.0	165		Beutler (1986)
Gomphidae						
Asiagomphus melaenops (Selys)	1960		53.0	181		Kurata (1971)
Asiagomphus melaenops	1969		58.9	141	0.05	Kurata (1971)
Asiagomphus pryeri (Selys)	1996		41.5	193	0.05	T. Aoki (in press)
Gomphus vulgatissimus (Linnaeus)	1980		41.8	182	0.05	Beutler (1986)
Gomphus vulgatissimus	1984		46.2	169		Beutler (1986)
Gomphus vulgatissimus	1986		44.6	184		Schwaller & Eigenheer (1989)
Gomphus vulgatissimus	1987		51.8	170		Schwaller & Eigenheer (1989)
Gomphus vulgatissimus	1989		45.8	118		Kern (1992)
Onychogomphus forcipatus (Linnaeus)	1989		36.5	192	0.001	Herden (1990)
Ophiogomphus cecilia (Fourcroy)	1993		54.7	128		Werzinger & Werzinger (1994)
Ophiogomphus cecilia	1991		55.7	140		Müller (1995)
Ophiogomphus cecilia	1993		44.2	156		Müller (1995)
Stylurus nagoyanus (Asahina)	1977		29.2	192	0.001	Ishida (1982)
Stylurus oculatus (Asahina)	1967		27.0	141	0.001	Kurata & Morozumi (1969)
Stylurus oculatus	1968		38.3	107	0.05	Kurata & Morozumi (1969)
Stylurus oculatus	1963		29.5	129	0.001	Inoue (1979)
Libellulidae						
Crocothemis erythraea (Brullé)	1992		54.8	146		Agüero-Pelegrin & Ferreras-Romero (1994)
Leucorrhinia pectoralis (Charpentier)	1984		45.8	131		Beutler (1986)
Sympetrum sanguineum (Müller)	1991		46.4	138		Hoess (1993)
Zygoptera						
Coenagrionidae						
Ischnura elegans (Vander Linden)	1990		50.8	183		Jahn (1991)
Ischnura verticalis (Say)	1961		34.4	189	0.001	Kormondy & Gower (1965)
Pyrrhosoma nymphula (Sulzer)	1987		56.0	109		Krüner (1989)
Lestidae						
Austrolestes colensonis (White)	1977-78	C	46.5	114		Deacon (1979)
Lestes rectangularis Say	1960		29.8	104	0.001	Kormondy & Gower (1965)

1)
A: Friedland; B: Sandgrube Beeskow "Friedländer Berg" Weiher 1; C: Isaac's Pond (Lowland); D: Sandgrube Beeskow "Friedländer Berg"
Weiher 2; E: pond C; F: Stückerkehle bei Oberhausen EM, Probestrecke 1; G: Lake Sarah-ls; H: pond B; I: Tagebausee; J: Stückerkehle bei Oberhausen EM, Probestrecke 2; K: Site A; L: Site C; M: Pond A; N: Pond B; O: Aufforstung; P: Waldecke; (S): summer generation

Table 2. Sex ratios based on totals between 200 and 299. Conventions as in Table 1.

199<N<300

Taxa	Coll. season[1]	Coll. loc.	% males	N	Chi-squared test, P<	Reference
Anisoptera						
Aeshnidae						
Aeshna cyanea	1984	D	48.2	218		Beutler (1986)
Aeshna cyanea	1995	E	47.3	260		Inden-Lohmar (1997)
Aeshna mixta	1982		50.0	254		Beutler (1986)
Aeshna subarctica elisabethae	1994		45.4	295		W. Clausen (pers. comm.)
Aeshna subarctica elisabethae	1995		47.5	217		W. Clausen (pers. comm.)
Anaciaeschna martini (Selys)	1994		17.1	252	0.001	Taketo (1994)
Corduliidae						
Cordulia aenea	1971		52.8	248		Ubukata (1974)
Cordulia aenea	1972		43.0	223	0.05	Ubukata (1981)
Cordulia aenea	1974		40.5	205	0.01	Ubukata (1981)
Somatochlora arctica (Zetterstedt)	1984		35.9	284	0.001	Sonehara (1985)
Gomphidae						
Asiagomphus melaenops	1961		50.2	203		Kurata (1971)
Gomphus flavipes Charpentier	1992		43.0	256	0.05	MŸller (1995)
Gomphus vulgatissimus	1985		55.2	290		Schwaller & Eigenheer (1989)
Gomphus vulgatissimus	1991		30.7	228	0.001	MŸller (1995)
Gomphus vulgatissimus	1994		36.6	279	0.001	MŸller (1995)
Gomphus vulgatissimus	1995	F	50.2	237		Westermann et al. (1995)
Ictinogomphus clavatus (Fabricius)	1966		43.0	293	0.05	Kurata & Morozumi (1969)
Ictinogomphus clavatus	1968		38.0	263	0.001	Kurata & Morozumi (1969)
Ophiogomphus cecilia	1992		56.4	234	0.05	Werzinger & Werzinger (1993)
Stylurus nagoyanus	1980		44.6	294		Ishida (1982)
Stylurus nagoyanus	1981		34.1	217	0.001	Ishida (1982)
Stylurus oculatus	1964		44.0	252		Kurata & Morozumi (1969)
Libellulidae						
Libellula quadrimaculata Linnaeus	1991		47.2	250		Hoess (1993)
Sympetrum vicinum (Hagen)	1961		37.9	261	0.001	Kormondy & Gower (1965)
Zygoptera						
Coenagrionidae						
Coenagrion hastulatum (Charpentier)	1996		55.3	219		Befeld et al. (1997)
Coenagrion puella (Linnaeus)	1977		52.0	248		Karaman (1987)
Coenagrion puella	1990		48.9	221		Jahn (1991)
Pyrrhosoma nymphula	1985		50.9	283		Bennett & Mill (1993)
Pyrrhosoma nymphula	1986		49.6	272		Bennett & Mill (1993)
Lestidae						
Austrolestes colensonis	1976-77	C	53.3	210		Deacon (1979)
Austrolestes colensonis	1976-77	G	57.8	211	0.05	Deacon (1979)
Lestes dryas Kirby	1990		45.2	250		Jahn (1991)
Lestes eurinus Say	1966		52.0	296		Lutz (1968)
Lestes vigilax Selys	1969		46.0	252		Ingram (1976)
Lestes viridis (Vander Linden)	1990		54.4	228		Jahn (1991)

1)
Abbreviations as listed in Table 1.

Table 3. Sex ratios based on totals exceeding 299. Conventions as in Table 1.
N>299

Taxa	1) Coll. season	1) Coll. loc.	% males	N	Chi-squared test. P<	Reference
Anisoptera						
Aeshnidae						
Aeshna affinis Vander Linden	1996		49.9	425		Bernard & Samolag (1997)
Aeshna cyanea	1993	H	49.7	716		Inden-Lohmar (1997)
Aeshna cyanea	1993	E	48.1	561		Inden-Lohmar (1997)
Aeshna cyanea	1994	H	46.4	1227	0.05	Inden-Lohmar (1997)
Aeshna cyanea	1994	E	47.2	754		Inden-Lohmar (1997)
Aeshna cyanea	1995	H	42.2	325	0.01	Inden-Lohmar (1997)
Aeshna nigroflava Martin	1971		47.9	1571		Ubukata (1974)
Aeshna subarctica elisabethae	1962		48.3	785		Schmidt (1964)
Anaciaeschna isosceles	1991		58.8	323	0.01	Leyshon & Moore (1993)
Anax imperator	1939		47.0	610		Fastenrath (1950)
Anax imperator	1951		49.3	1951		Corbet (1957, 1962)
Anax imperator	1952		47.2	4368	0.001	Corbet (1957, 1962)
Anax imperator	1953		49.0	2944		Corbet (1957, 1962)
Anax imperator	1982	I	47.1	1386	0.05	Beutler (1986)
Anax imperator	1983	I	46.5	512		Beutler (1986)
Anax imperator	1984	I	48.4	1993		Beutler (1986)
Anax imperator	1991		64.4	842	0.001	Hoess (1993)
Anax junius	1967(S)		46.8	495		Trottier (1971)
Anax parthenope julius Brauer	1995		46.0	424		Taketo (1995)
Boyeria irene (Fonscolombe)	1992		46.5	1079	0.05	Ferreras-Romero & Corbet(1995)
Cordulegastridae						
Cordulegaster boltonii (Donovan)	1992		47.2	1091		Ferreras-Romero & Corbet(1995)
Corduliidae						
Cordulia aenea	1975		43.5	490	0.01	Ubukata (1981)
Cordulia aenea	1976		42.0	395	0.01	Ubukata (1981)
Epitheca bimaculata (Charpentier)	1966		42.9	329	0.01	Sonehara (1982)
Epitheca cynosura (Say)	1960		44.3	1681	0.001	Lutz & McMahan (1973)
Epitheca cynosura	1961		38.9	537	0.001	Lutz & McMahan (1973)
Epitheca cynosura	1962		48.9	722		Lutz & McMahan (1973)
Epitheca cynosura	1963		49.6	1109		Lutz & McMahan (1973)
Epitheca cynosura	1964		52.7	783		Lutz & McMahan (1973)
Gomphidae						
Asiagomphus melaenops	1963		61.0	890	0.001	Kurata (1971)
Asiagomphus melaenops	1965		50.5	376		Kurata (1971)
Asiagomphus pryeri	1994		38.9	339	0.001	Aoki (1994)
Gomphus exilis Selys	1960		47.3	1054		Lutz & McMahan (1973)
Gomphus exilis	1961		49.9	501		Lutz & McMahan (1973)
Gomphus exilis	1962		47.5	1707	0.05	Lutz & McMahan (1973)
Gomphus exilis	1963		47.9	2591	0.05	Lutz & McMahan (1973)
Gomphus exilis	1964		45.6	630	0.05	Lutz & McMahan (1973)
Gomphus flavipes	1989		40.6	1191	0.001	Müller (1995)
Gomphus flavipes	1990		51.0	514		Müller (1995)
Gomphus flavipes	1991		54.3	427		Müller (1995)
Gomphus flavipes	1993		49.0	594		Müller (1995)

Gomphus flavipes	1994		40.1	411	0.001	Müller (1995)
Gomphus pulchellus Selys	1990		50.7	523		Suhling (1991)
Gomphus pulchellus	1991		50.1	383		A. Langenbach in litt.
Gomphus vulgatissimus	1990		43.9	643	0.01	Kern (1992)
Gomphus vulgatissimus	1991		46.8	653		Kern (1992)
Gomphus vulgatissimus	1992		48.8	461		Kern (1992)
Gomphus vulgatissimus	1993		47.0	640		Kern (1992)
Gomphus vulgatissimus	1994		46.4	584		Kern (1992)
Gomphus vulgatissimus	1990		44.7	599	0.05	Müller (1995)
Gomphus vulgatissimus	1992		47.1	348		Müller (1995)
Gomphus vulgatissimus	1993		72.4	413	0.001	Müller (1995)
Gomphus vulgatissimus	1995	J	50.0	636		Westermann et al. (1995)
Ictinogomphus clavatus	1964		39.6	1033	0.001	Kurata & Morozumi (1969)
Ictinogomphus clavatus	1965		36.7	4915	0.001	Kurata & Morozumi (1969)
Ictinogomphus clavatus	1967		41.2	405	0.001	Kurata & Morozumi (1969)
Onychogomphus forcipatus	1991		45.8	391		Brendel (1992)
Onychogomphus uncatus (Charpentier)	1991		43.9	1409	0.001	Schütte (1992)
Onychogomphus uncatus	1992		49.0	1758		Kleemeyer (1994)
Onychogomphus uncatus	1993		41.2	650	0.001	Suhling (1995)
Onychogomphus uncatus	1994		51.6	1912		Jakob (1995)
Onychogomphus viridicostus (Oguma)	1964		48.9	931		Kurata (1968)
Onychogomphus viridicostus	1965		49.2	1069		Kurata (1968)
Ophiogomphus cecilia	1989		47.3	575		Müller (1995)
Ophiogomphus cecilia	1990		54.7	406		Müller (1995)
Sieboldius albardae Selys	1969		61.8	631	0.001	Aida (1972)
Stylurus annulatus (Djakonov)	1962		47.5	354		Inoue (1979)
Stylurus annulatus	1963		47.1	350		Inoue (1979)
Stylurus oculatus	1965		54.9	421	0.05	Kurata & Morozumi (1969)
Stylurus oculatus	1966		44.6	307		Kurata & Morozumi (1969)
Libellulidae						
Brachythemis contaminata (Fabricius)	1973-74		46.0	2976	0.001	Mathavan & Pandian (1977)
Brachythemis contaminata	1974-75		47.7	1962	0.05	Mathavan & Pandian (1977)
Deielia phaon (Selys)	1964		43.3	975	0.001	Kurata & Morozumi (1969)
Deielia phaon	1965		37.7	618	0.001	Kurata & Morozumi (1969)
Deielia phaon	1966		43.4	785	0.001	Kurata & Morozumi (1969)
Diplacodes trivialis (Rambur)	1973-74		45.9	2960	0.001	Mathavan & Pandian (1977)
Diplacodes trivialis	1974-75		46.0	3339	0.001	Mathavan & Pandian (1977)
Leucorrhinia dubia (Vander Linden)	1959	K	44.5	1707	0.001	Pajunen (1962)
Leucorrhinia dubia	1959	L	48.8	588		Pajunen (1962)
Leucorrhinia dubia	1960	K	48.5	967		Pajunen (1962)
Leucorrhinia dubia	1960	L	44.1	431	0.05	Pajunen (1962)
Leucorrhinia pectoralis	1989		45.3	475	0.05	Wildermuth (1994)
Leucorrhinia rubicunda (Linnaeus)	1959	K	49.2	311		Pajunen (1962)
Leucorrhinia rubicunda	1960	L	39.5	423	0.001	Pajunen (1962)
Leucorrhinia rubicunda	1985		45.8	906	0.05	Soeffing (1990)
Leucorrhinia rubicunda	1986		41.0	602	0.001	Soeffing (1990)
Leucorrhinia rubicunda	1987		47.8	592		Soeffing (1990)
Orthetrum cancellatum (Linnaeus)	1991		44.6	2163	0.001	Hoess (1993)
Orthetrum sabina (Drury)	1973-74		45.7	975	0.01	Mathavan & Pandian (1977)
Orthetrum sabina	1974-75		47.7	438		Mathavan & Pandian (1977)

Pantala flavescens (Fabricius)	1973-74		48.7	992		Mathavan & Pandian (1977)
Pantala flavescens	1974-75		45.5	786	0.05	Mathavan & Pandian (1977)
Sympetrum striolatum (Charpentier)	1991		46.3	3719	0.001	Hoess (1993)
Sympetrum vulgatum (Linnaeus)	1991		46.2	1953	0.001	Hoess (1993)
Trithemis annulata (Beauvois)	1992		52.1	1721		Agüero-Pelegrin & Ferreras-Romero (1994)
Trithemis festiva (Rambur)	1973-74		53.3	2790	0.001	Mathavan & Pandian (1977)
Trithemis festiva	1974-75		48.7	1385		Mathavan & Pandian (1977)
Zygoptera						
Coenagrionidae						
Coenagrion hastulatum	1987		50.1	985		Lösing (1988)
Coenagrion puella	1979		48.2	1451		Karaman (1987)
Coenagrion puella	1991		47.4	340		Hoess (1993)
Enallagma cyathigerum (Charpentier)	1991		47.6	1442		Hoess (1993)
Enallagma hageni (Walsh)	1969		51.9	626		Ingram & Jenner (1976)
Ischnura verticalis	1989		51.2	1824		Baker et al. (1992)
Pyrrhosoma nymphula	1986	M	54.6	1014	0.01	Gribbin & Thompson (1991)
Pyrrhosoma nymphula	1986	N	53.1	1099	0.05	Gribbin & Thompson (1991)
Pyrrhosoma nymphula	1984		51.6	1426		Bennett & Mill (1993)
Pyrrhosoma nymphula	1994	O	50.4	1794		Inden-Lohmar (1997)
Pyrrhosoma nymphula	1994	P	51.6	1524		Inden-Lohmar (1997)
Pyrrhosoma nymphula	1995		51.7	3190		Inden-Lohmar (1997)
Xanthocnemis zealandica (Mc Lachlan)	1976-77	C	50.6	1635		Deacon (1979)
Xanthocnemis zealandica	1977-78	C	51.4	773		Deacon (1979)
Xanthocnemis zealandica	1976-77	G	51.1	4270		Deacon (1979)
Xanthocnemis zealandica	1977-78	G	50.2	4983		Deacon (1979)
Lestidae						
Lestes sponsa (Hansemann)	1984		45.7	495		Zettelmeyer (1986)
Lestes sponsa	1990		47.0	364		Jahn (1991)
Lestes viridis	1985		52.7	385		Cordero (1988)
Lestes viridis	1991		49.4	723		Hoess (1993)
Sympecma fusca (Vander Linden)	1991		51.7	1320		Hoess (1993)

1) Abbreviations as listed in Table 1.

Before including records from 11 other sources we had to recalculate sex ratios to allow for mathematical error, inclusion of unsexed exuviae or combination of two or more emergence periods.

Notwithstanding the approach adopted by Corbet (1962: p. 117) in the first review of sex ratio in Anisoptera, we recommend against inclusion of records based on parts of a year, and on several habitats combined, for non-seasonal tropical species. Although sex ratios obtained by Corbet (1962: table VII) for tropical species, based on collections made on several occasions and at several places on Lakes Albert and Victoria in East Africa (Table 5), conform well with expectation based on values for temperate Anisoptera that

meet the stated criteria, we consider it premature to *assume* that sex ratio in non-seasonal species is independent of time of year or place. We therefore recommend that such records are not treated as comparable with those from sites, be they tropical or temperate, where emergence is seasonally restricted and where the criteria listed above can be applied. In contrast, the results of Mathavan & Pandian (1977) for five species of Libellulidae are acceptable for purposes of the present review, having been obtained where emergence was seasonal (following the north-east monsoon in Tamil Nadu, India) and confined to about eight months each year. The possibility cannot be excluded, however, that one species studied by Mathavan & Pandian (1977), namely *Pantala flavescens*, had an emergence curve which, being somewhat bimodal, might have reflected the emergence of some individuals which were the progeny of those that emerged earlier in the same emergence season.

Data that meet our criteria have been segregated among Tables 1-3 according to size of collection (the minimum acceptable total being 100) on the assumption that larger collections provide results in which greater confidence can be placed. Because for statistical reasons ratios cannot be averaged, we present data graphically in Figs. 1-16 in a form that we believe is likely to reveal central tendency, range and variability in records of this kind. Sex ratios are expressed as percentage males of the total.

For each record where the ratio differs "significantly" from 50% (as indicated by a value of P of 0.05 or less, using conventional chi-squared analysis) we record the value of P, although we do not thereby imply that a ratio of 50% constitutes expectation. Indeed there is now ample justification for assuming that, in many species, the usual sex ratio is not 50%.

Table 4. Frequency distributions of sex ratios according to family (Cordulegastridae omitted). This table is based on all records in Tables 1-3, and therefore features multiple records for some species.

	% males: lower limit of class														
	15	20	25	30	35	40	45	50	55	60	65	70	a	b	c
Aeshnidae	1				2	4	28	4	2	1			83	13	4
Corduliidae					2	7	2	2					85	4	3
Gomphidae			3	2	7	16	20	14	4	2		1	70	15	7
Libellulidae					3	6	20	3					91	17	10
Coenagrionidae				1			5	16	2				25	8	5
Lestidae			1				6	5	1				54	8	3

a = % of records < 50% males
b = No. of species
c = No. of genera

In Table 5 we include data that, though not complying with our criteria, may later prove to be informative.

Authorities for scientific names of species included in Tables are given on the first occasion of mention there, and otherwise on first mention in the text.

Table 5. Sex ratios of non-seasonal tropical species. Data are from table VII in Corbet (1962); entries for each species combine records made on several occasions and at several place on Lakes Albert and Victoria in East Africa.

Nonseasonal species

Taxa	Coll. period	% males	N	Chi-squared test, P<	Reference
Anisoptera					
Corduliidae					
Macromia picta Selys	1954-61	47.7	455		Corbet (1962)
Gomphidae					
Crenigomphus renei Fraser	1954-61	47.2	1109		Corbet (1962)
Ictinogomphus ferox (Rambur)	1954-61	44.5	312		Corbet (1962)
Paragomphus hageni (Selys)	1954-61	41.7	386	0.01	Corbet (1962)
Libellulidae					
Brachythemis leucosticta (Burmeister)	1954-61	41.1	304	0.01	Corbet (1962)
Zygonyx natalensis (Martin)	1954-61	47.0	936		Corbet (1962)

Results

Species represented by records that meet our criteria are predominantly those which have large, readily identifiable exuviae and that exist in conveniently large numbers in water bodies of moderate size. Because of this bias, conclusions applying to Odonata in general can only be tentative until further information reveals if, and to what extent, it is appropriate to combine data for different taxa. In the meantime, aggregate distributions appear to show a level of consistency that deserves comment.

The data, presented in the Tables and Figures, encompass 50 species of Anisoptera, from 25 genera and 5 families, and 16 species of Zygoptera, from 8 genera and 2 families.

At the level of the suborder (Figs 1, 2) and family (Figs 3, 4, 6, 8, 9), except Corduliidae and Libellulidae, and perhaps one species (*Gomphus vulgatissimus*, Fig. 16), variability appears to be distinctly less among larger collections, a trend already discernible in collections narrowly exceeding 299 exuviae.

Data in Figs 1-3 support the conclusion that the sex ratio of Anisoptera (45% of records within 45-50% males) is lower than that of Zygoptera (57% within 50-55% males). For collections exceeding 299 exuviae, 89% of records of Anisoptera lie within 40-55% males and all records of Zygoptera lie within 45-55% males. In both suborders outliers are

virtually absent in collections clearly exceeding 1000 exuviae, the only one being *Ictinogomphus clavatus* (36.7% males). This aberrant record need not qualify the conclusion (regarding lower sex ratio of Anisoptera) as it applies to Aeshnidae and Libellulidae because data (Fig. 3) indicate that sex ratio is relatively low in Corduliidae (69% of records within 35-45% males) and Gomphidae (33% within 35-45% males), and that in both families sex ratio varies widely among species and localities, even in collections exceeding 500 exuviae, e.g. *Epitheca cynosura* 38.9-52.7% males (N = 537-1681, 5 collections, 1 locality) and *Onychogomphus uncatus* 41.2-51.6% males (N = 650-1758, 4 collections, different localities).

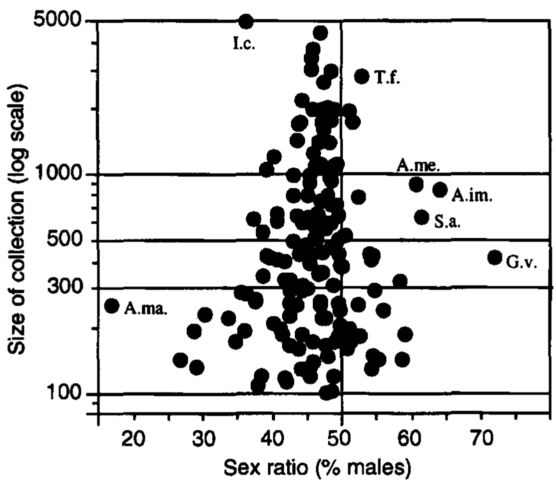


Figure 1. Anisoptera: records of sex ratio according to size of collection (log scale). A.im., *Anax imperator*; A.ma., *Anaciaeschna martini*; A.me., *Asiagomphus melaenops*; G.v., *Gomphus vulgatissimus*; I.c., *Ictinogomphus clavatus*; S.a., *Sieboldius albardae*; T.f., *Trithemis festiva*.

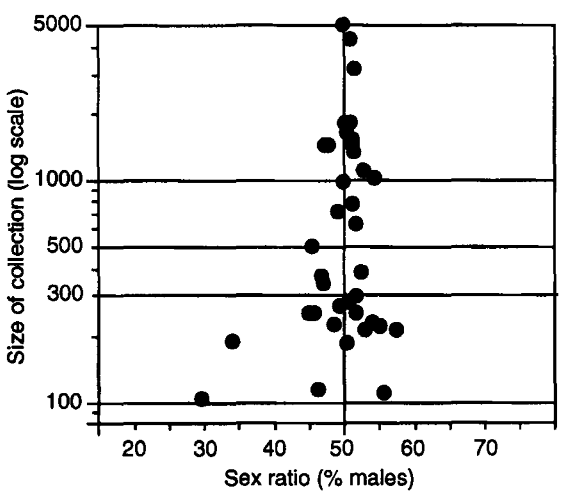


Figure 2. Zygoptera: records of sex ratio according to size of collection (log scale).

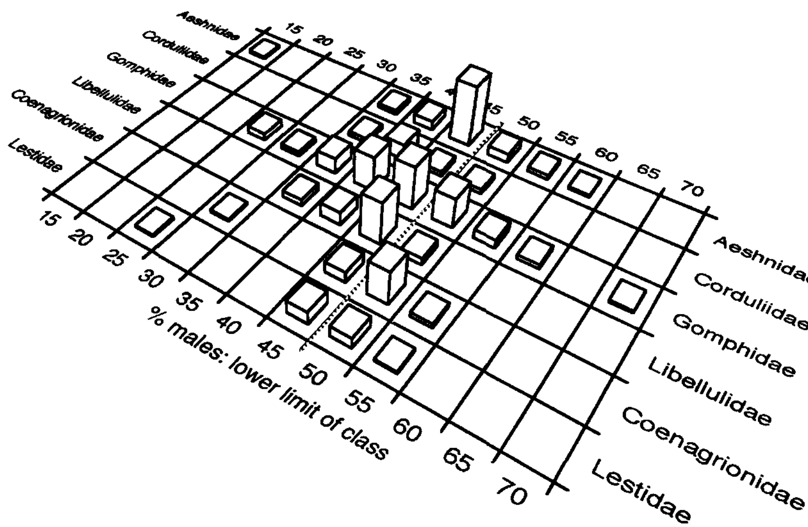
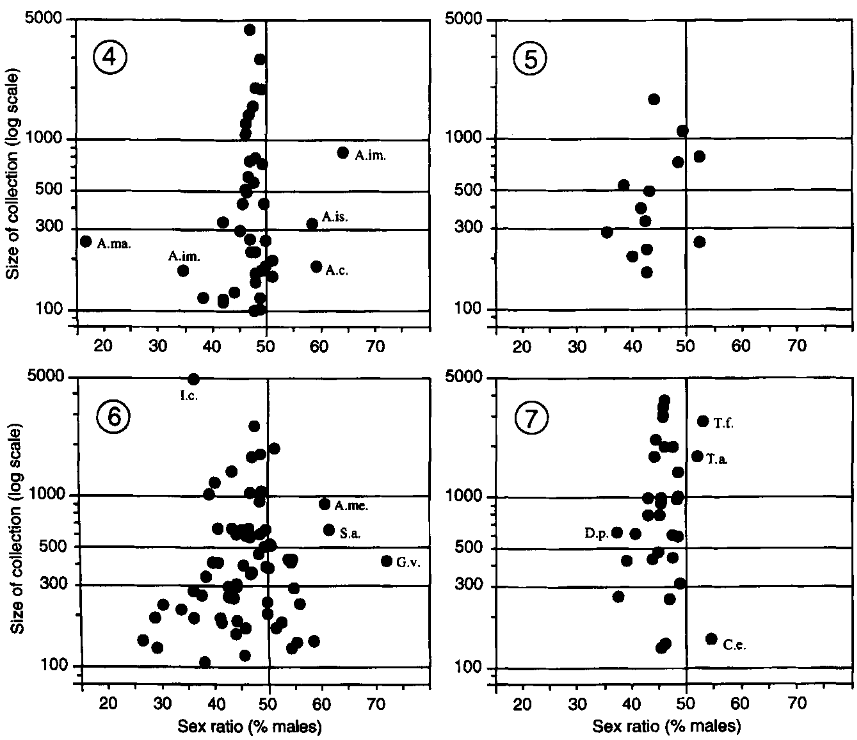


Figure 3. Odonata: sex ratio according to family and frequency, based on entries in Tables 1-3 (Cordulegastridae omitted). For frequencies (height of bars) see Table 4. The dotted line indicates a sex ratio of unity, i.e. 50% males.



Figures 4-7. Records of sex ratio according to size of collection (log scale). 4, Aeshnidae; 5, Corduliidae; 6, Gomphidae; 7, Libellulidae. A.c., *Aeshna cyanea*; A.is., *Anaciaeschna isosceles*; C.e., *Crocothemis erythraea*; D.p., *Deielia phaon*; T.a., *Trithemis annulata*. Other abbreviations as in Figure 1.

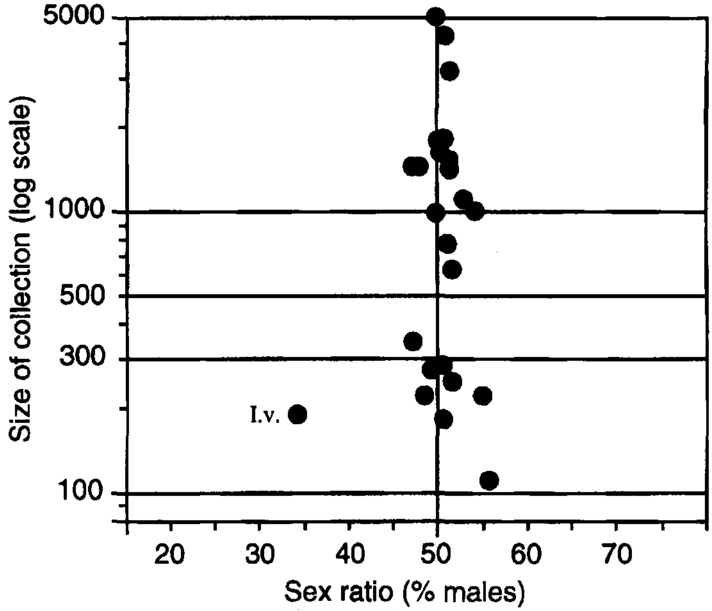


Figure 8. Coenagrionidae: records of sex ratio according to size of collection (log scale). I.v., *Ischnura verticalis*.

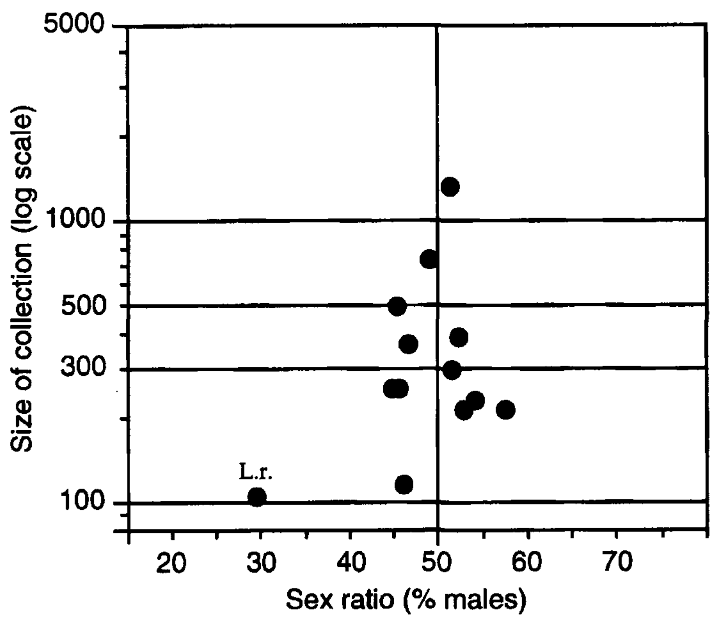
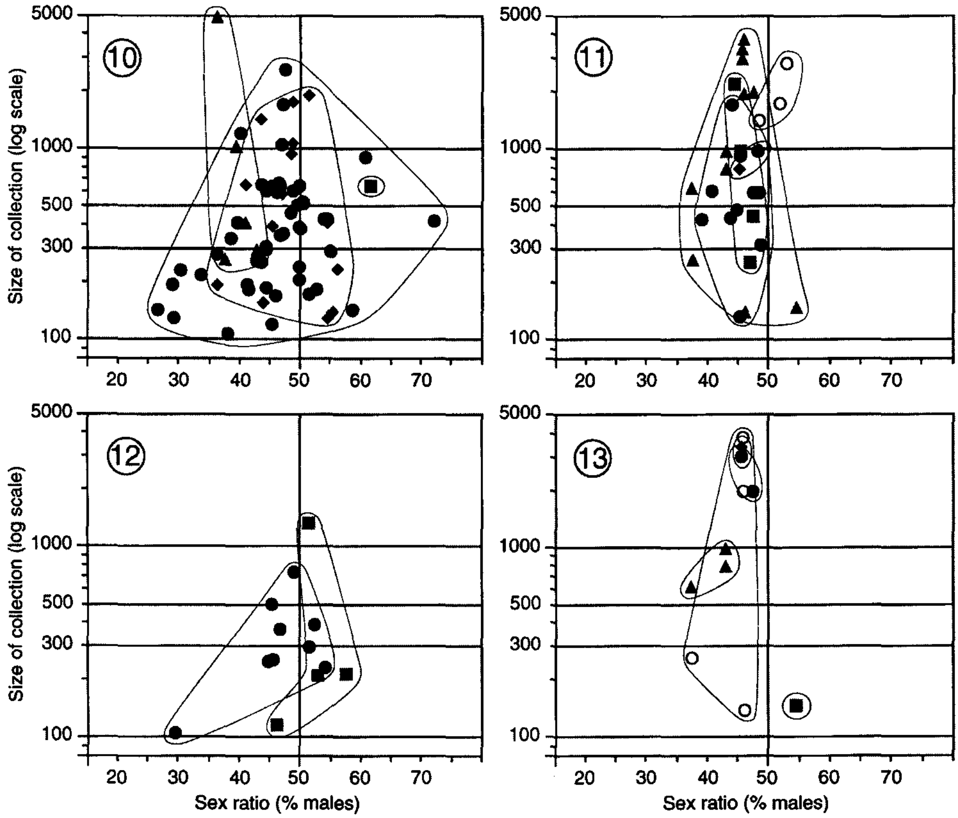


Figure 9. Lestidae: records of sex ratio according to size of collection (log scale). L.r., *Lestes rectangularis*.



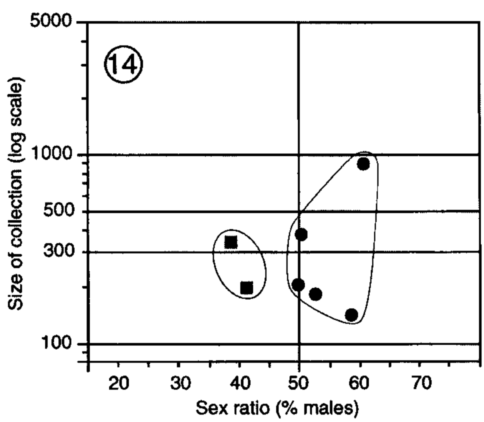
Figures 10-13. Records of sex ratio by subfamily or genus according to size of collection (log scale). 10, Gomphidae: ●, Gomphinae; ■, Hageniinae; ▲, Lindeniinae; ◆, Onychogomphinae. 11, Libellulidae: ●, Leucorrhiniinae; ■, Libellulinae; ▲, Sympetrinae; ◆, Trameinae; O, Trithemistinae. 12, Lestidae: ●, Lestinae; ■, Sympecmatinae. 13, Sympetrinae: ●, *Brachythemis*; ■, *Crocothemis*; ▲, *Deielia*; ◆, *Diplacodes*; O, *Sympetrum*.

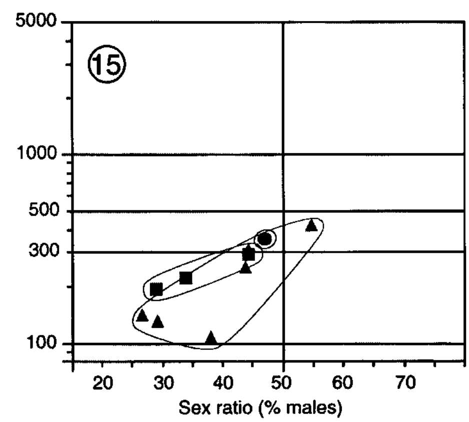
In contrast, some species show remarkably little variation, e.g. *Pyrrhosoma nymphula* 53.1 and 54.6% males in the same year in two ponds 40 m apart (N >1000 in each) and *Xanthocnemis zealandica* 50.2-51.4% males (N = 773-4983, 4 collections, two at a site 30 m, and two at a site 579 m above mean sea level). Other species may show little variation except for one aberrant record, e.g. *Anax imperator* 46.5-49.3% males (N = 512-4368, 7 collections, 3 localities) and 64.4% males (N = 842, a fourth locality).

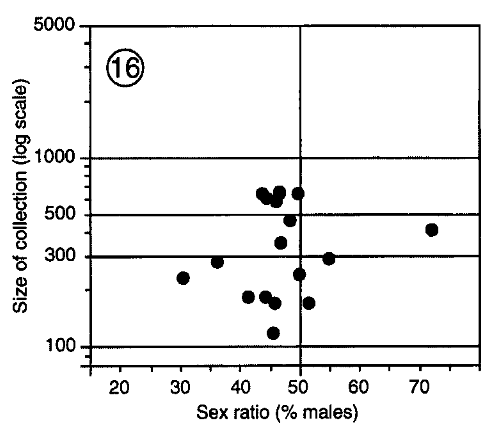
Discussion

Sex determination in Odonata is genetic, not environmental (see Conover & Heins, 1987), and is the subject of a searching study by Kiauta (1969) whose relevant conclusions are as follows. The original mode of sex determination in the order is of the XO/XX type, the male being the heterogamic sex, and exists in all primary complements, regardless of chromosome number, i.e. the degree of specialisation exhibited by the taxa concerned. In secondary complements a neo-XY sex determination occurs, where the original X has been fused with an autosome. Such an occurrence, which is often irreversible and which can be found in some cells (or stages) but not in others of a single individual, seems unrelated to a taxon's inferred phylogeny. If stabilised, the neo-XY condition tends to evolve further, as in Gomphidae, into a secondary XO type.

Pending evidence to the contrary, one must assume that the sex-determining mechanisms documented for Odonata produce a sex ratio of unity in the newly fertilised zygote. It is therefore plausible to hypothesise that any variability and imbalance in the sex ratio at emergence reflect differential mortality during the aquatic stages.







Figures 14-16. Records of sex ratio by species according to size of collection (log scale). 14, *Asiagomphus*: ●, *A.melaenops*; ■, *A.pryeri*. 15, *Stylurus*: ●, *S.annulatus*; ■, *S.nagoyanus*; ▲, *S.oculatus*. 16, *Gomphus vulgatissimus*.

The analysis by Lawton (1972) for Zygoptera showed that, in the species he studied, sex ratio does not change significantly during the last five larval instars (i.e. those during which larvae can be sexed by use of external characters). If this situation applies generally, causes of imbalance could reasonably be sought during the egg or early larval stages. Beyond this, one can only speculate, bearing in mind that predation plays a major role in larval mortality (see Johnson, 1991) and that microhabitats occupied by larvae vary widely and correlate closely with larval form and behaviour, especially among Anisoptera; such microhabitats also change during larval ontogeny (see Corbet, 1999). These considerations suggest one arena in which male and female larvae might sustain differential mortality. In this connexion, it is noteworthy that agonistic ("territorial") interactions occur primarily among male, but not female, larvae of *Calopteryx splendens* (Harris) (Ryazanova, 1988).

Whether or not the causes of sex-ratio imbalance in Odonata can be discovered, it can be stated securely: that, in species included in Tables 1-3, sex ratio at emergence often exhibits an imbalance; that the extent of the imbalance differs among families; and that sex ratio can vary greatly or very little within a species. It can be stated further that, having regard to the widely different mating frequencies between males and females and often intense sexual selection among males (see Corbet,1999), imbalances of the extent reported here are unlikely to have any significant effect on the reproductive potential of the adult population, although the size of the next generation might be reduced when, as happens occasionally (e.g. *Gomphus vulgatissimus*, Fig. 16), the number of females is exceptionally low.

If future work reveals consistent differences in sex ratio between species or higher taxa, a reasonable approach might be to seek correlations between sex ratio and larval microhabitat, especially among Anisoptera (Corbet, 1999:table A.5.7), between sex ratio and habitat (i.e. type of water body) and also between sex ratio and voltinism, according to the prediction that the longer the more susceptible sex is exposed to larval mortality factors, the greater is the imbalance in its sex ratio at emergence. It must be said, however, that this prediction is not supported by the greater number of females in the second (univoltine) peak of emergence of *Anax imperator* in an otherwise semivoltine emerging population (Corbet, 1957). Because of wide variability in ecological conditions, between habitats and years, we consider it unlikely that any detectable correlations will be clear-cut. So the causes of sex-ratio imbalance in Odonata are likely to remain elusive.

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